

## Behavior of Male Desert Hackberry Butterflies, *Asterocampa leilia* (Nymphalidae) at Perching Sites used in Mate Location

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**Abstract.** Males of the desert hackberry butterfly (*Asterocampa leilia*) occupy and defend perches at mate encounter sites adjacent to the larval foodplant. When returning from an interaction with a conspecific, a male selects a perch within about 2 m<sup>2</sup>, surrounding his original perch. These perching sites are surrounded by areas of significantly lower vegetation than other areas around the larval foodplant.

Over the course of the morning activity period the perching behavior of the males changes in ways that are quantitatively documented. Early in the morning males perch on the ground with the wings open facing away from the sun. Later they perch facing the same direction but with the wings closed. Later still they perch on vegetation a little less than a meter above the ground with wings closed, facing out of the plant on which they are perched. The perch preferences and orientation of males when perched are discussed in light of the hypothesis that males maximize their ability to detect males and females flying in their vicinity, yet maintain tolerable body temperatures.

### Introduction

In many insect species, males occupy and defend encounter sites as part of their mate-locating effort (Thornhill and Alcock, 1983). The selection of these sites and the behavior of males at them is thought to be structured in ways that increase their contacts with receptive females. Some studies have shown that males that defend encounter sites have a higher rate of contacting receptive females than males that do not defend, and that the most attractive areas, whether defended or not, are those with the highest arrival rate of receptive females (Borgia, 1982; Courtney and Parker, 1985; Forsyth and Montgomerie, 1987; Lederhouse, 1982; Severinghaus et al., 1981; Shelley, 1987; Wickman, 1985). However, there have been few studies that have quantified in detail the behavior of males within an encounter site or the physical characteristics of these sites to see if males select sites and orientations with characteristics that might enhance their ability to detect females that fly by.

In the desert hackberry butterfly (*Asterocampa leilia* Edwards), males actively defend perching sites that are on or adjacent to the larval foodplant, the desert hackberry tree (*Celtis pallida* Torrey; Austin, 1977; Rutowski and Gilchrist, 1988). From their perches, which can be on the ground or the hackberry, males fly out at conspecifics; intruding males are chased, and females are courted. Males use these sites to detect newly-emerged virgin females as they first fly from their pupation sites

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on or near the larval foodplant (Rutowski and Gilchrist, 1988). Perch sites are most frequently occupied and most intensely defended in the midmorning hours in central Arizona. In addition, some sites used by males are highly attractive and are occupied on a daily basis during the flight season. These attributes make *A. leilia* a good species for a study of perching behavior and perching site characteristics.

Males visually detect females and other males. Hence, in this study we have focused on those aspects of male perch selection and perching behavior within a defended encounter site that might affect a male's visual field. To begin, we present measures of the size of perching sites based on the distribution of perches adjacent to several hackberry trees. These data give some indication of the constancy of perch selection both within and between males. Next, we describe the distribution of vegetation around perching sites to see if views from the perches that males select are more expansive than those from other spots around the hackberry tree. Finally, we quantify how perched males are oriented with respect to the sun, the larval foodplant, and other variables that might affect a male's view. The results are discussed in light of the expectation that males behave in ways that enhance their ability to detect females flying near their perching sites.

For clarity we define a *perch* as a specific point on the ground or on a hackberry tree where a male has landed and a *perching site* as an area, typically within an encounter site at the perimeter of a hackberry tree, that encompasses the perches selected by one or more males. Lastly, a *sortie* is when a male leaves a perch to chase a flying conspecific or other animal, or a thrown object, and then returns to the perch site.

## Methods

**Study sites.** The two study sites in central Arizona have been previously described (Rutowski and Gilchrist, 1988; Rutowski et al., 1988). One was off of the Bush Highway near the Salt River northeast of Mesa, Arizona. The second was east of State Route 87 (Beeline Highway) where the highway crosses Sycamore Creek south of Sunflower, Arizona. In both areas the predominant trees were paloverde (*Cercidium* spp.), mesquite (*Prosopis* spp.), and hackberry. The study was conducted between April and June in 1988 and 1990.

**Location of perches within a perching site.** We documented the distribution of perches selected within a defended site to define the size and location of the perching site. We identified and mapped 6 sites (SC1-SC6) where males were regularly seen perched in the Sycamore Creek area. Sites SC1, SC2, and SC3 were located in a dry stream bed, while the other three were located along sandy corridors in vegetation in the broad floodplain of Sycamore Creek. A 10 m baseline was established along the stream bed or corridor at each site and was used to map the locations of perches, prominent vegetation, rocks, etc.

At each of the six sites we obtained the location of five perches for each of 10 males. These observations were made between 0815 and 1045 MST between 17 and 26 May 1988. For each male we noted where on the site he was perched when first seen and where he perched when he returned from his next four sorties, which were either stimulated by an animal flying by (usually a conspecific) or by

a rock thrown over the male, or occurred for no apparent reason. If we lost sight of a male during a sortie the observation on that male was terminated.

This protocol was developed from our knowledge of male behavior which suggested that males typically spend 30 min or less at a site before moving on to another, especially early in the activity period (Rutowski and Gilchrist, 1988). Hence, 5 sorties were taken as a reasonable representation of perch selection by a male at a site. Moreover, the rate of interactions is greatest early in the activity period and falls off quickly as the morning progresses. Tossing rocks helped us stimulate sorties at times when passing conspecifics were relatively rare. There was no evidence that males were traumatized by the rocks; they chased the rocks briefly before returning to perch.

For the set of 5 perches for each male within a site we calculated the distance between sequential perches and the distance between the place the male was first seen perched and each of the 4 subsequent perches. Then, using a digitizing pad and maps of each male's perches we measured the area of the polygon that included all perches for males that used at least three different perches. If a male used only one or two perches, area measurements were not possible.

**Male perch sites relative to the hackberry tree.** Occupied perching sites were identified by first finding a perched male and noting the location of his perch. We then threw rocks over him and elicited sorties. If after each of three sorties the male selected a perch within one meter of his original perch we identified the male as the resident of an occupied perching site. We then examined various aspects of the perch at which he was first seen. These observations were only made on males initially observed perched in full sun.

We first determined if males preferentially perched on a particular side of a hackberry tree, such as the south side. To do this we characterized the position of the perch at which a male was first seen with respect to the compass bearing from the center of the nearest hackberry to the perch.

Next, we tested the prediction that males select perches that are in sites with a relatively large view by describing the distribution of vegetation around a perch in an occupied site.

From the original perch we measured the distance to the nearest vegetation over one meter high at 0, 45, 90, 135, 180, 225, 270, and 315 degrees relative to the bearing from the perch into the center of the nearest hackberry plant. We then made the same measurements for a spot the same distance from the perimeter of the hackberry tree as the perch, but at a point around the perimeter randomly selected by coin toss. The point was selected from 8 possible points at 45 degree increments starting at magnetic north. A paired t-test was used to evaluate the magnitude and direction of the differences in area between male-selected and randomly-selected sites.

**Male orientation when perching.** Male perch sites were identified by the three-perches-within-1-m criterion as described above. For the first perch observed we noted where the male was perched (ground or vegetation), the direction the male faced, the distance of the male from the nearest hackberry plant, the direction from the male to the sun's azimuth, the time of day, and the direction to the center of the nearest hackberry tree.

**Directional measurements and statistical evaluation.** Directional measurements in this study were made with a hand-held compass relative to magnetic north or to the nearest hackberry tree depending on the purpose of the measurement. Summaries and analyses of directional measurements were made using techniques described in Batschelet (1981).



All parametric summary statistics are given as mean  $\pm$  standard deviation. The results of all statistical tests are evaluated at the 0.05 level of significance.

**Results**

**PERCHING SITE CHARACTERISTICS: SIZE**

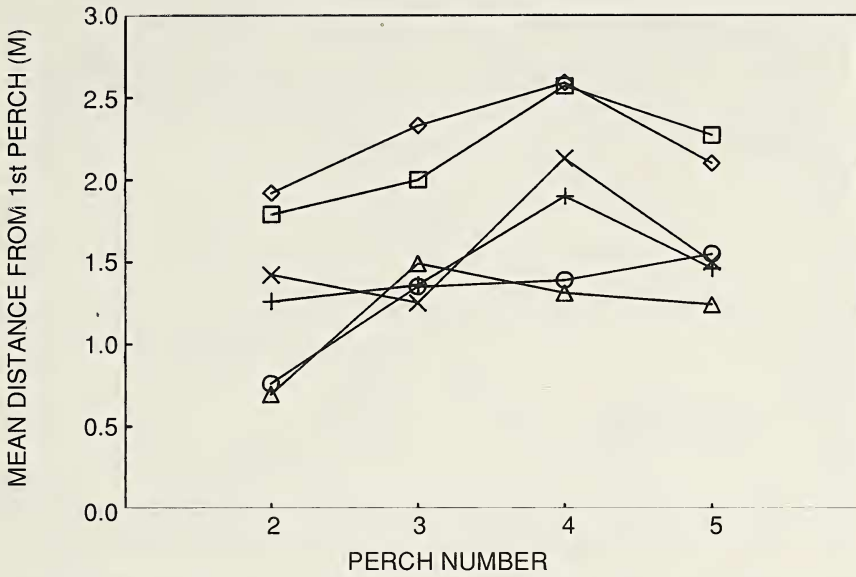
After a sortie, a male did not usually return to exactly the same perch. In the 240 sorties that we observed, males returned to the same spot only 39 times. Thirty-six (60%) of the 60 males whose five perches were recorded perched in a new location after each sortie. The remaining 24 males when returning from a sortie alit on a perch they had previously used at least once. Of the males that used less than 5 different perches, 7 used 4, 7 used 3, 7 used 2, and 3 males used only a single perch.

Still, over a series of five perches males tended to return to the same general area. The average distance between sequential perches observed at each site was about 1 meter (Table 1). The perches selected after each of four sorties were within 2 m of the original perch on a site (Table 1). Fig. 1 shows the distance subsequent perches fell from the first perch a male selected. Although there was a slight trend for males to increase their distance from the first perch with each sortie this trend was usually reversed with the fifth perch.

Across the 6 sites at Sycamore Creek, the average area that included all perches for males that used three or more different perches was  $1.58 \pm 1.57 \text{ m}^2$  ( $n = 50$ ). The summary statistics for the area measurements

**Table 1.** The distances moved and areas including all perches for males observed at the 6 Sycamore Creek study sites. Sample size for each mean is 10.

	Site					
	SC1	SC2	SC3	SC4	SC5	SC6
Average distance from 1st perch (m)						
Mean	2.16	1.49	2.25	1.18	1.58	1.26
STD	1.34	0.98	1.39	1.4	1.31	1.0
Min	0.66	0.42	0.29	0	0.31	0.112
Max	5.51	3.44	4.75	3.81	4.15	2.98
Average distance moved (m)						
Mean	1.6	1.09	1.74	0.87	1.24	0.95
STD	0.84	0.68	0.78	0.91	0.87	0.88
Min	0.31	0.32	0.43	0	0.1	0.05
Max	3.34	2.66	3.29	2.95	2.76	3.05
Area including all perches for an individual male (m2)						
Mean	2.22	1.52	1.95	1.55	0.85	0.97
STD	1.49	2.10	1.17	1.72	0.8	1.74
Min	0.3	0.07	0.02	0.39	0.13	0.05
Max	4.43	7.23	4.09	5.06	2.15	4.66
N	10	10	10	6	8	6



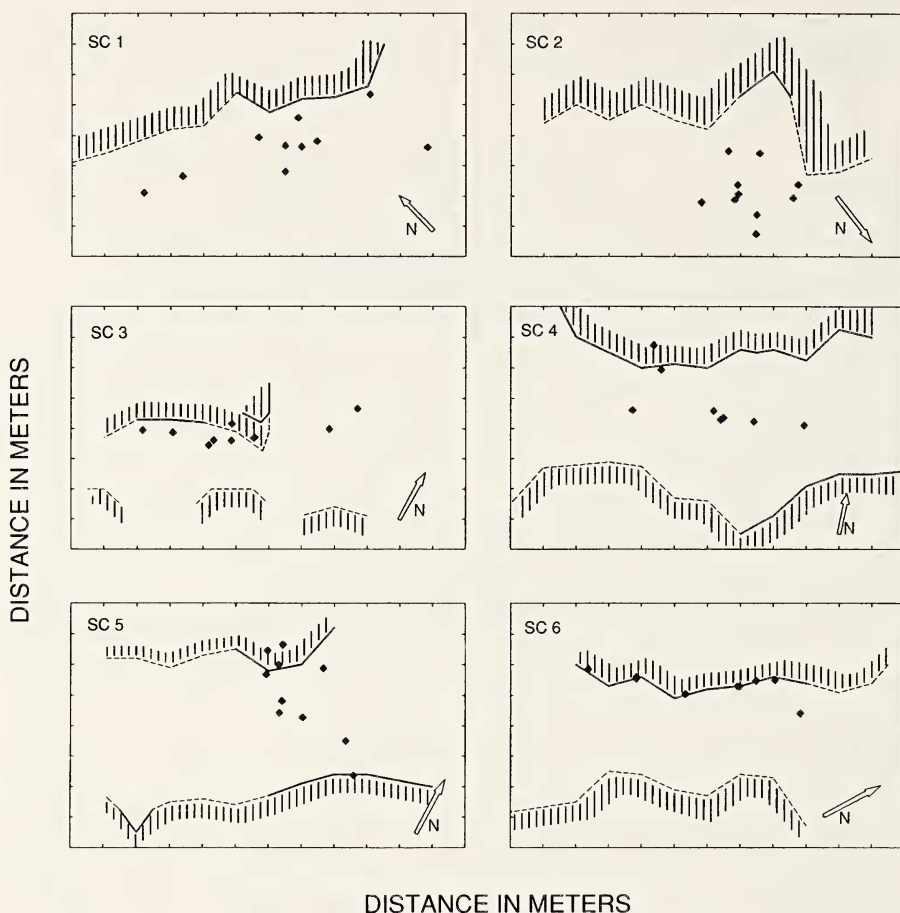
**Figure 1.** The distance subsequent perches were from the first perch. This is plotted for the 10 males at each site that were observed to perch five times. Each point represents the mean for the 10 males at that site. Legend: SC1 (square), SC2 (+), SC3 (diamond), SC4 (triangle), SC5 (x), SC6 (circle).

from each site are given in Table 1. These statistics exclude the 10 males that used less than 3 different perches and so constitutes an overestimate. The size of the perching areas did not differ between sites for males that used 3 or more perches (ANOVA,  $F = 0.97$ , 5,44 df,  $p = 0.47$ ). The mean location for each of the 10 males observed to perch 5 times is shown for each site in Fig. 2.

**PERCHING SITE CHARACTERISTICS: PLACEMENT**

How were perches placed with respect to the compass bearing from the middle of the nearest hackberry tree? The distributions of perches around the nearest larval foodplant relative to magnetic north are shown for perches on the ground and on the plant in Fig. 3. Males were randomly distributed with respect to the compass bearing out of the nearest hackberry tree regardless of perch substrate (ground: Rayleigh test,  $r = 0.093$ ,  $n = 26$ ,  $p > 0.78$ ; hackberry: Rayleigh test,  $r = 0.316$ ,  $n = 23$ ,  $p > 0.1$ ); hence, perching areas are not located in any particular direction, north east, south, or west, from the nearest hackberry.

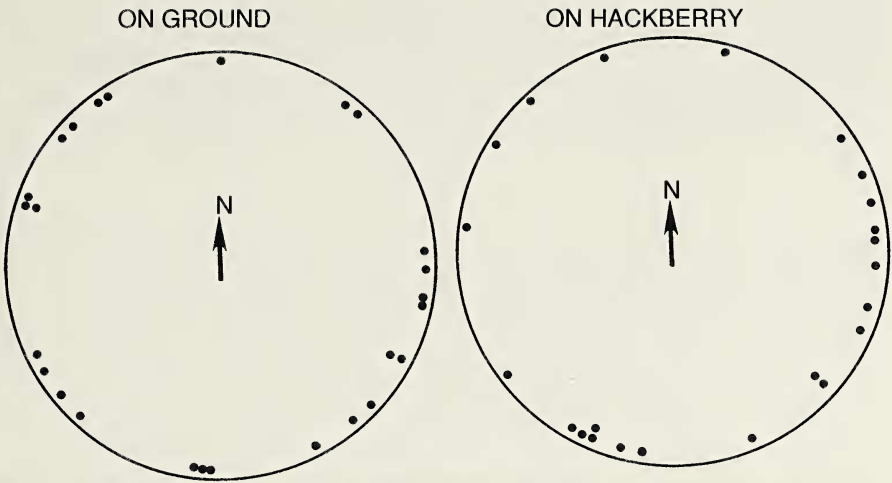
Males perch in areas relatively free of vegetation. The size of the open area surrounding a perched male ( $57.6 \pm 6.04 \text{ m}^2$ , range 23 - 85.9  $\text{m}^2$ ) was significantly larger than that surrounding randomly-selected points adjacent to the hackberry tree ( $12.6 \pm 16.19 \text{ m}^2$ , range 0 - 41.7  $\text{m}^2$ ; paired t-test = 9.647, 9 df,  $p = 0.0005$ ).



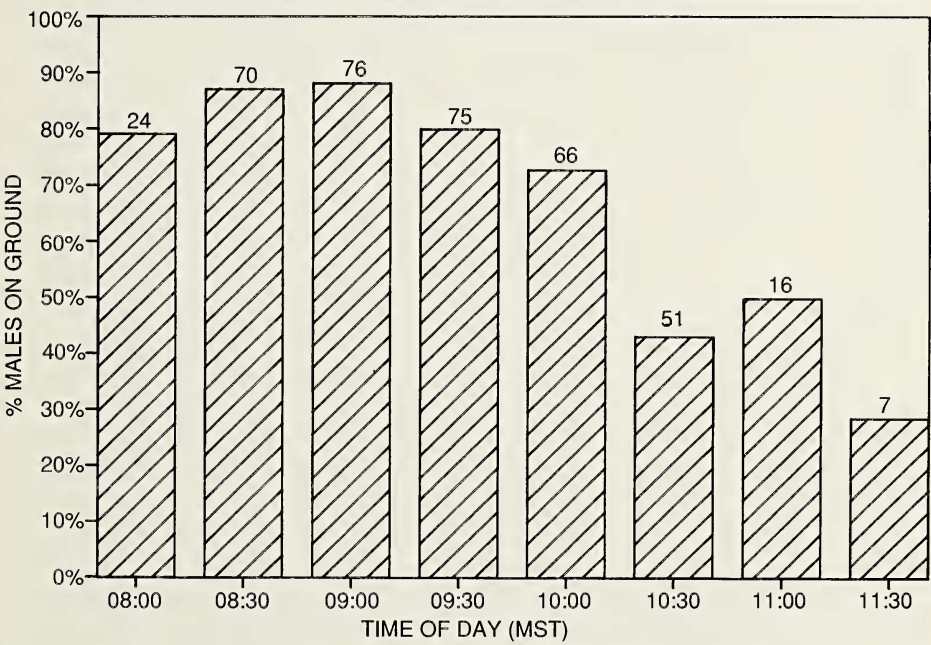
**Figure 2.** Maps of sites SC1 through SC6 showing the mean location for each of 10 males that were observed to perch five times on the site. Solid lines indicate the borders of hackberry trees, dashed lines indicate the edge of other vegetation, except in SC1 where the dashed line indicates the edge of a small cliff, and the crosshatching indicates the direction into the vegetation.

### MALE ORIENTATION WHEN PERCHED

What factors influence the direction a male faces when he lands at a perch? We examined three possibilities: (1) the type of perch (ground or vegetation), (2) the direction to the nearest hackberry, and (3) the direction to the sun's azimuth. Early in the day virtually all males perched on the ground or on low rocks, sticks or other objects (e.g. dried cow excrement) adjacent to a hackberry tree. However, as the morning progressed an increasing proportion of males perched on the tree about 1 m above the ground (Fig. 4;  $\chi^2 = 51.5$ , 7 df,  $p < 10^{-5}$ ). Perches on the ground were  $1.37 \pm 0.81$  m (range, 0.1 - 3.4 m;  $n = 26$ ) from the perimeter of the nearest hackberry. Perches on hackberry were  $0.87 \pm 0.23$  m (range, 0.1 - 1.4 m;  $n = 52$ ) from the ground.

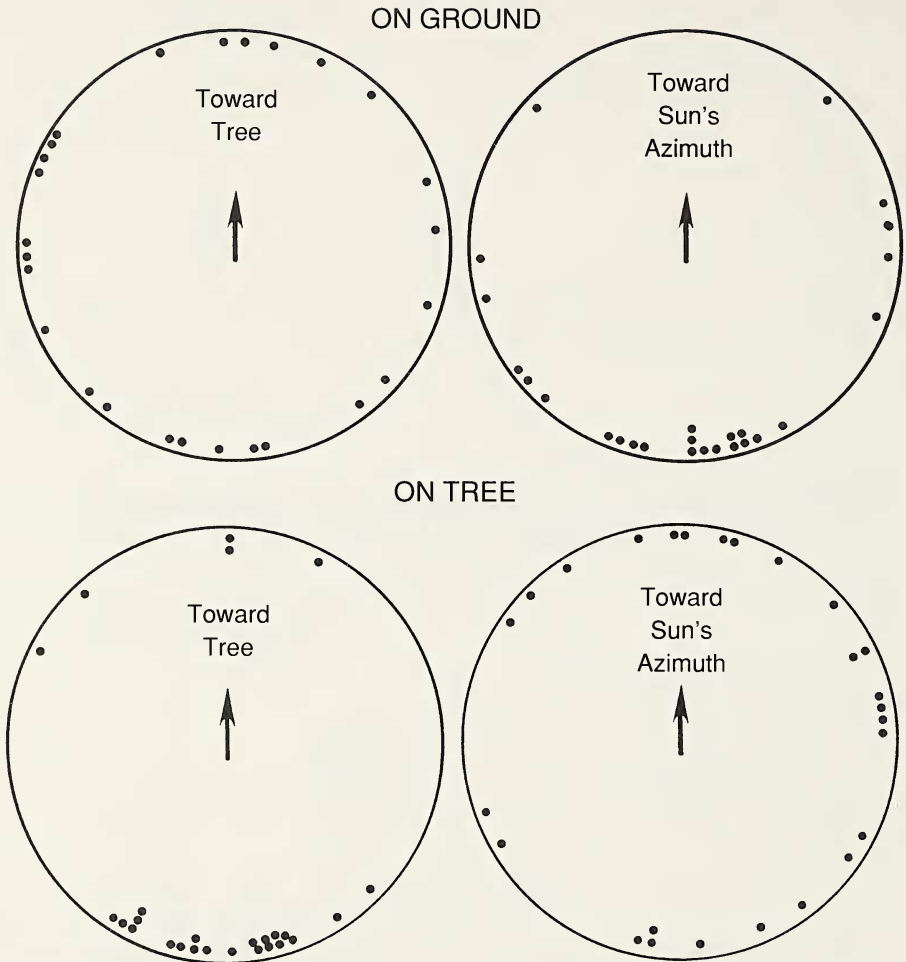


**Figure 3.** The compass bearing from the center of the nearest hackberry tree to the perch for perches on the ground (n = 26) and on the tree (n = 23).



**Figure 4.** The change in the proportion of individuals perched on the ground as a function of time of day. The number above each bar is the number of males observed at that time.

Fig. 5 shows the direction perched males faced relative to the sun's azimuth and the nearest hackberry tree for males perched on the ground (n = 26) and on the hackberry (n = 23). The direction males faced when perched on the ground was significantly correlated with the direction to the sun (Circular rank correlation,  $r^2 = 0.23$ ,  $p < 0.01$ ) but was not



**Figure 5.** Directions faced by males perched on the ground ( $n = 26$ ) and on the hackberry tree ( $n = 23$ ) relative to the sun's azimuth and relative to the center of the hackberry plant.

correlated with the direction to the nearest hackberry tree (Circular rank correlation,  $r^2 = 0.003$ ,  $p > 0.99$ ). Hence, on the ground males faced away from the sun (mean difference between direction male faced and bearing to the sun = 177 degrees) and showed no special orientation to the plant. Because of this negative orientation to the sun and the restricted range of values for bearing to the sun's azimuth the distribution of directions males faced was significantly non-random (Rayleigh test,  $r = .64$ ,  $p < 0.001$ ).

In contrast, when perched on the tree, the distribution of compass bearings males faced was random (Rayleigh test,  $r = 0.17$ ,  $p > 0.05$ ). However, the direction they faced was significantly correlated with the direction into the hackberry (Circular rank correlation,  $r^2 = 0.34$ ,  $p <$



0.002) and was not correlated with the direction to the sun (Circular rank correlation,  $r^2 = 0.16$ ,  $p > 0.7$ ). Males perched on the hackberry, then, faced out of the plant (mean difference in male bearing and bearing from male to plant center = 190.4 degrees) and displayed no special orientation to the sun.

## DISCUSSION

The data reveal several features of the perches at encounter sites used by *A. leilia* males in mate location that have been suggested by previous authors (Austin, 1977; Rutowski and Gilchrist, 1988), but have not been previously documented. First, males select perching areas in open areas adjacent to the larval foodplant. Second, the perches selected are low, either on the ground or within one meter of the ground. Third, the perches selected at a site by a male tend to be within a meter or two of one another. Fourth, male body orientation changes in a correlated fashion with changes in perch substrate over the course of a morning. Early on, males perch on the ground facing away from the sun, at first with the wings spread and later with the wings closed. Later in the morning, they switch to perches on the larval foodplant and face out of the plant.

These changes in perch and body orientation preferences at encounter sites suggest that two primary selective factors have shaped the evolution of male perching behavior within an encounter site. The first is selection favoring perch and body orientation preferences that produce a visible field with characteristics that enhance the detection of passing conspecifics (potential mates and intruding males) and predators. We assume for the time being that being perched on or next to a desert hackberry tree will produce the highest rate of encounters with receptive females and focus this discussion on whether or not males behave in ways that maximize the likelihood of detecting those passing animals.

The problem faced by perched males is that of detecting small, rapidly-moving objects passing nearby which is certain to be affected by the features of the background against which the objects are viewed. Studies of visual system operation in insects and other animals suggests that a bright, uniform background such as the sky or distant vegetation is best for detection of small moving objects (Hailman, 1977; Horridge, 1977). The apparent preferences of males for perches in open areas would avoid obscuring vegetation and maximize the part of the visual field occupied by sky. In addition, facing away from the sun may avoid excessively bright backgrounds against which detection of small moving objects might be difficult.

However, selection favoring preference for open areas should be affected by selection favoring the avoidance of extreme body temperatures. Butterflies, like most insects, are ectotherms which means their body temperatures are greatly affected by solar radiation incident on their body and convective heat gain from the environment (for review, see: Clench, 1966; Kingsolver, 1985). Nonetheless, in a broad range of

ambient air temperatures butterflies maintain their body temperature within a restricted range through behavioral adjustments affecting heat gain. In *A. leilia*, male behavior at perch sites may reflect thermoregulatory activities.

Early in the morning, solar heat gain can be important for maintaining body temperatures that exceed the air temperature and permit the butterflies to be active (Kingsolver, 1983a,b). Hence, at this time of day, exposure to solar radiation can be advantageous and may have favored males that perch in locations and orientations (facing away from the sun with the wings open ("dorsal basking")) that enhance solar heat gain.

Later in the morning, incident solar radiation as well as high air temperatures near the substrate may favor postural adjustments that reduce heat gain like those seen in other butterflies (Rawlins, 1980) to avoid intolerable body temperatures. Facing away from the sun with the wings closed minimizes the surface area exposed to solar radiation and so reduces heat gain by this avenue.

As the morning passes and air and substrate temperatures rise, the ground must often become too hot to use as a perch location as has been seen in the males of a territorial digger wasp (O'Neill and O'Neill, 1988). In early summer we have measured substrate surface temperatures late in the activity period as high as 54 degrees C. At this time males move into the shade (Austin, 1977) and up onto vegetation where it is presumably cooler. Their body orientation is no longer relative to the sun when perched on the plant, but instead is relative to the plant. They may face out of the plant to maintain a view of the sky in as much of their visual field as possible.

The sequence of perch site preferences displayed suggests that males prefer ground perches out a meter or so from the edge of the larval foodplant but that thermoregulatory concerns may drive males to less satisfactory perch locations. Currently we are attempting to test this scenario by gathering three types of information. One is data on the flight paths of females and males as they pass near perching sites. Perhaps the preference changes over the morning reflect changes in the flight paths and altitudes at which conspecifics are likely to enter a male's perching site. The second is data on the thermal biology of *A. leilia*. We are measuring male body temperatures under different conditions and characterizing the thermal environment. We expect substrate preferences and body orientations to be structured in a way that keeps body temperature within the thermal preferences of *A. leilia*. The third type of data are on the sensitivities of the visual system in *A. leilia* and the visual field characteristics that permit detection of conspecifics from the greatest possible distance from a male's perch. These data should permit a more complete understanding of the variables that influence the selection of perches in species such as *A. leilia* that use perches to make contact with airborne resources such as mates or prey.

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